# A TETRAPTERYX STAGE IN THE ANCESTRY OF BIRDS

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## Part I.—Introduction.

Our knowledge of the genealogy of birds is in inverse ratio to the abundance of these organisms on the earth today. We know of quite primitive forms of fish—both fossil and living—of reptiles and of mammals. But of living birds, those which show encouragingly primitive characters exhibit also an equal number of extremely specialized ones.

Some six or seven million years ago in the Cretaceous Period we know that there lived creatures which undeniably deserve the name of birds. Ichthyornis was a strong-flying, tern-like type with numerous, recurved teeth, and Hesperornis was also toothed, but practically wingless, essentially a diving bird, and on shore probably more helpless than a seal.

In the Jurassic, let us say four million years earlier, two more or less complete fossil skeletons have been discovered, and an odd feather or two of the famous Archaeopteryx, the *sine qua non* of avian genealogy. Teeth again we find in a very lizard-like head; delicate, weak, wing bones supporting a good-sized but rounded wing, and the fore limb terminating in three well devel-

oped, clawed fingers; a long, vertebrated tail, with a pair of excellent feathers sprouting at each joint and a pair of feet admirably adapted for perching. The unmistakably reptilian traces give weight to Huxley's superclass Sauropsida.

Slight though this evidence is compared to the imposing array of fossil reptiles and mammals, it nevertheless provides an unmistakable lead in the direction of small, arboreal, lizard-like creatures along a still earlier line of ancestry.

I do not wish in this paper to discuss, except in one respect, the various characters of Archaeopteryx. I am working out a life-sized restoration of a flock of seven of these winged creatures of ancient times and not until this is completed shall I feel confident of expressing any new views on the general character of this much discussed creature.

My present thesis, while in a way independent of Archaeopteryx, yet is given force in dynamic presentation by consideration of this strange creature.

Perhaps the most astounding thing about this being is the perfection of its wing and tail feathers. Without going into reasons, I am convinced that Archaeopteryx was a bird of very limited powers of flight. I am not certain that it could flap at all and if it could, its aerial feats hardly equalled those of a modern tinamou or domestic fowl. It certainly had very excellent powers of scaling, and in this direction probably exceeded any modern flying squirrel or lemur.

Whether this be conceded or not is aside from my point, which is concerning the origin of this wing. Our knowledge of the workings of evolution often enable us to visualize the growth and later development of an organ, its subsequent specialization and perhaps ultimate degeneration, while we utterly fail to explain its origin or early development. It is well within the limits of gradual cumulative variation to admit the change from an Archaeopteryx to a modern wing. The wing bones increase in size and those of the hand coalesce, the fingers become mittened in flesh and tendon; the primaries increase in number creeping out upon the phalanges, and the muscles wax stronger, become

larger and find adequate place for attachment upon a greatly enlarged sternum. But how could the wing have reached its Archaeopteryx stage of development?

In Mexican or Neotropical jungles bordering rivers and streams it is a common sight to see great iguanas resting high among the upper branches and foliage. When suddenly alarmed or toward sunset, these great reptiles do not bother to climb slowly down along their back trails which they so laboriously mounted earlier in the day. They recklessly launch out into mid-air and with legs widely extended, body flattened, toes clutching at the empty air, they hurtle downward, landing with a crash into the underbrush or with a splash in the water. Perhaps their flattening may help somewhat to break their fall, but I doubt if this would save their life were they to land upon hard ground. Twice, in fact, I have seen iguanas after a bad take off, half turn in the air, so that they landed in the water on their side or in one case actually upside down, when the reptile seemed stunned for a minute before it turned over and swam from sight. Here, it seems to me, we have a very probable *anlage* of scaling flight, as ultimately perfected in Archaeopteryx.

But if we arm our imaginations with a prejurassic, parachuting lizard on the one hand, and Archaeopteryx on the other, we still have a hiatus which no logical combining of proportional characters will bridge. Suppose if you will that the scales along the posterior edge of the fore leg and those along the tail begin to lengthen. Carry these along to a fair development and then start the hopeful organism out into mid-air and it will prove an utter failure. The scaly primaries may be sufficient to support the front part of the body, but the tail scales would certainly not suffice both to balance and to bear up the remainder of the lizard. The result would be a woeful sagging which must bring instant disaster,—a herpetological Darius Green which could not hope to leave offspring to work out their fossil destiny. The development of scaling flight with nothing to correspond to the great lateral and caudal membranes of flying mammals is inconceivable. Something is needed to bridge over the very beginnings of the parachuting wing function. Even a flying fish has two nodes of aerial support during its brief essay into a thinner

medium. It spreads capable little planes aft as well as forward. Cut off the pelvic fins and I imagine it would plop hindmost into the water almost as soon as it emerged. Some such accessory has always seemed to me necessary if we are to complete our lizard-to-Archaeopteryx line of ascent.

Recently, while examining the fresh body of a four-days'-old White-winged Dove in the New York Zoological Park, I observed on its almost naked body a remarkable development of sprouting quills across the upper part of the hind-leg, and extending toward the tail across the patagium just behind the femur. A second glance showed that this was no irregular or abnormally precocious development of part of the femoral pterylum, but a line of primary-like sheaths, many of which had a very definitely placed *covert*. The iguana-Archaeopteryx puzzle flashed through my mind and I at once followed up the clue thus given. For the two sketches illustrating my idea of the Tetrapteryx Stage of alar evolution I am indebted to Mr. Dwight Franklin.

## Part II.—Pelvic Wing.

The detection of this interesting character occurred in August, too late for observations on many forms of nestling birds. I embody in the following notes all that I have been able to gather together on the existence of this curious *pelvic* or *femoral wing*.

### White-Winged Dove.

*Melopelia asiatica* (Linn.)

Several of these birds had been reared during the present season in the special breeding cages of the New York Zoological Park. On August 19 a four-days'-old squab, the only nestling of a second brood, was found dead in its nest and brought to me.

Its leaden grey body appeared almost bare, being covered sparsely with the characteristic short, greyish white, filamentous down. Three areas showed precocious development of contour feathers, the wing proper, the pelvic wing and the tail. In the former, twenty-two flight feathers were developed, of which ten were primaries averaging 10 mm. in length, nine were secondar-

FIG. 8. DOMESTIC PIGEON SQUAB

Showing great development of the pelvic wing. The leg is flexed, hence this atavistic wing is folded

FIG. 9. SQUAB OF WHITE-WINGED DOVE

Four days old, with wing and leg extended, showing the wide spread pelvic wing

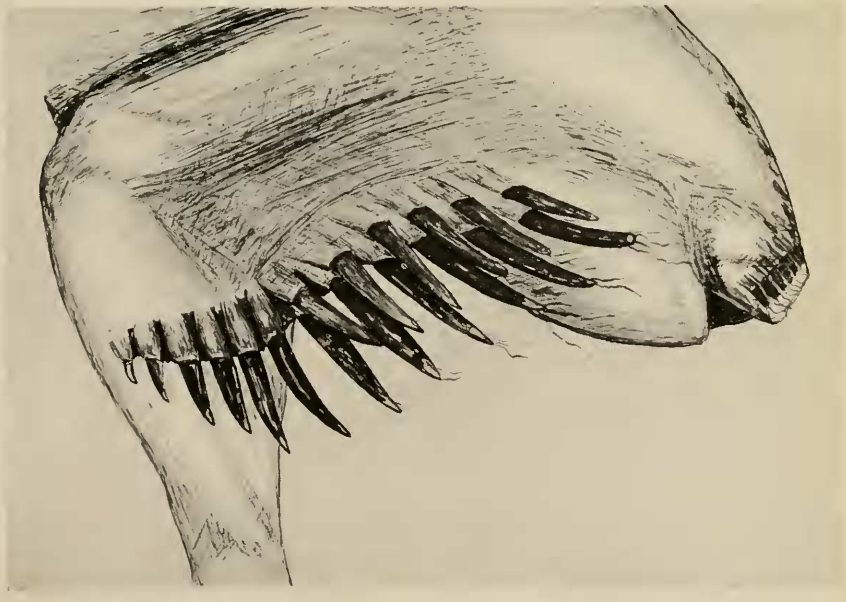

FIG. 10. DETAIL OF PELVIC WING OF WHITE-WINGED DOVE, SHOWN IN FIG. 9

The wing consists of twelve flights and six coverts

ies, grading inward from 8 to 5 mm., and three were tiny tertiaries. The primaries had only a single row of strongly developed, greater coverts. Four rows of secondary coverts were sprouting, the central ones pure white, indicating the future color pattern of the wing.

Next in development to the wing proper, were the feathers of what, for lack of a better name, I call the pelvic wing. This seems inexplicable on any other hypothesis than the vestigial secondary plane, which must have been of the utmost importance in the ancestral scaling flight.

This area begins on the anterior outer edge of the crus or leg proper, about one-third of the distance down from the knee. From this place it extends backward across the tibia almost at right angles to the backbone of the body, and, posterior to the femur, following the patagium, which lies between the leg and the body. It ends on the side of the body at an equal distance from the outer tail feather and from the pelvis between the acetabula. The areas are similar on both sides. There are twelve main or flight feathers. Feathers 1 to 6, extending from the body outward along the femoral patagium, all have a well-developed covert. The next six flights, numbers 7 to 12, lie close together on the flesh of the leg itself and show no signs of coverts. Counting from within outward these feathers measure as follows:

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Flights | 4.5 | 5.5 | 5.5 | 6 | 6 | 6 | 6 | 5.5 | 5 | 4 | 3 | 1 mm. |
| Coverts | 3.5 | 4 | 4 | 5 | 5.5 | 5.5 | | | | | | mm. |

The tail is much less advanced than the pectoral and pelvic wings, the rectrices and a single row of upper and another of under coverts being all equally advanced, measuring uniformly 3 mm. in length.

The pelvic wing tract is not apparent in the adult pterylosis of *Columba livia* as given by Nitzsch.[1] Its course is approximately along the upper margin of the crural tract, and continuing toward the tail well into the posterior part of the femoral or lumbar pterylum. In fact, the remaining pterylae of the body are very indistinctly demarcated in the down of this young squab.

[1]Pterylography, Nitzsch, Ed. by Sclater, 1867, plate VII, fig. 2.

## Domestic Pigeons.

*Columba livia* Bonn. (var.)

The pelvic alar tract is less regular in domestic pigeons than in wild birds, but is remarkably well developed. I give the results of my examination of four squabs taken at random from a large number.

A. The first was about a week old and the pelvic alar tract shows seven flights and four coverts. Always counting postero-anteriorly, the measurements in millimetres are as follows:

| Number of feather | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Length of flights | 6 | 7 | 8 | 6.5 | 5.5 | 3 | 2 |
| Length of coverts | 4 | 6 | 5 | 3 | | | |

B. A squab two weeks old shows ten flights. The posterior four are uniform; they have well developed upper coverts, which are small and lie close above the main feather. From the 5th onward the coverts give place to a row of under coverts. As we go forward, the flights and their coverts become less closely associated, until only the slight difference in elevation of the two most anterior pairs reveals their true relationship. The most anterior flight is isolated and covertless.

| Number of feather | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| Length of upper coverts | 5 | 5 | 5 | 3.5 | | | | | | |
| Length of flights | 6 | 7 | 8.5 | 9 | 7 | 6.5 | 6.5 | 5.5 | 4 | 3 |
| Length of under coverts | | | | | 4 | 3.5 | 4.5 | 4.5 | 4 | |

The precocious development of the feathers of this tract may be realized when compared with those of the true wing and tail in this same bird. The primaries and secondaries are all under five millimetres and the rectrices not more than two in length, while, as we have seen, seven out of ten of the pelvic flights are six millimetres or more, the general average over seven, and the maximum length nine millimetres.

C. A squab about three weeks old shows twelve pelvic flights. The arrangement of coverts is as follows:

Flight No. 1—small upper covert.
2—small upper covert.
3—down covert.
4—down covert.

5—small under covert.
6—down under covert.
7—large under covert.
8—large under covert.
9—large under covert.
10—large under covert.
11—no covert.
12—no covert.

D. A squab of five weeks shows that no additions occur at the posterior end of the pelvic alar tract. The next contour feathers to appear at this point form an ascending series of three, parallel to the backbone and at right angles to the pelvic alar tract. The first four flights with their upper coverts are well grown, far ahead of the rest of the body plumage. The coverts indeed are quite full grown, downy and white-shafted. As in squab C the flights from the 5th onward have under coverts. Altogether there are nine flights with coverts, and three anterior covertless ones.

While considering this newly observed character of pigeons, I thought of the feather-footed breeds and sent for a pair which I carefully dissected. I found no connection between these feather-footed and feather-legged domestic breeds and any unusual development of the pelvic alar tract. The feathers, which have been bred to great length, sprout from the scaly covering of the tarsus and phalanges and not from the leg proper or the femoral patagium, which is the seat of the character under consideration.

### Jacana.

*Jacana jacana* (Linn.)

In a half developed embryo the rectrices and pelvic alar feather papillae are well ahead of all others, even of the wing proper, and are the only ones which show any trace of pigment. In the pelvic alar tract there are four flights and three upper coverts, the anterior flight lacking a covert. In a second embryo, a day or two older, five flights and four coverts are visible in this tract.

### Great Horned Owl.

*Bubo virginianus* (Gmelin)

A brief examination of a living bird showed that the great development of soft plumage on the leg of this species arises from the pelvic alar tract. I was led to expect this from the pterylosis of *Strix bubo,* as given by Nitzsch.[1]

In his figure of *Columba livia*[2] there is, as I have said, no hint of the great development of the pelvic alar tract in the young bird, nor its remarkable disagreement with the lines of demarcation of the pterylae of the adult.

Judging merely from the pterylosis of the adult, many species of *Coraciiformes, Scansores* and *Piciformes* should show most interesting developments of this tract in the young birds.

### Archaeopteryx.

The foregoing observations on various species of living birds were inaugurated and completed before I took up the question in regard to Archaeopteryx. I realized that any trace of this pelvic alar tract which might be present in this ancient bird would be of superlative interest and significance, but until I carefully examined a full-sized photograph of the Berlin specimen I was not aware of the existence of feathers other than those on the wing and tail. I succeeded in finding distinct traces of strongly marked feathers on both sides of the tibia and of still larger feathers, lying between the pelvis and the bent back head. It seemed to me that such very evident traces could not have escaped the observation of other students of this wonderful fossil and I began a search of the literature. I was delighted to find that the tibial feathers had already aroused considerable discussion and I present this in abstract to show how variously the scientific mind has reacted to evidence of this character, unsupported by any other more modern proof. The London Archaeopteryx shows no trace of these feathers, so the whole evidence lies with the single fossil in the Berlin Museum.

[1]Pterylography, 1867, plate II, fig. 9.
[2]Id, plate VII, fig. 2.

The bibliography of this discussion is a short one:

VOGT:
"L'Archaeopteryx macrura.—Un intermédiaire entre les oiseaux et les reptiles." *Revue Scientifique,* 1879, (2) IX, p. 245.

EVANS:
"On portions of a Cranium and a Jaw of the Archaeopteryx," Preface to reprint, 1881, pp. 4-6.

DAMES:
"Ueber Archaeopteryx," *Palcontologischer Abhandlungen,* 1884, II. pp. 39-41.

ABEL:
*Grundzüge der Palaeobiologie der Wirbeltiere,* 1912, p. 343.

HEILMANN:
"*Vor Nuvaerende Viden om Fuglenes Afstamning,*" p. 14. Saertryk of Dansk Ornithologisk Forenings Tidsskrift.

Vogt is the first to mention the feathers whose impressions are visible on the leg of Archaeopteryx. "Le tibia était couvert de plumes dans toute sa longueur. L'Archaeopteryx portait donc des culottes, comme nos faucons, avec les jambes desquels sa jambe a le plus de resemblance, suivant M. Owen." [1]

J. Evans devotes several pages to these feathers and their significance, and a few years later Dames takes issue with him. The following sentences present Evans' view: " . . . . along the outer margin of the right tibia, there is a series of eight or possibly nine feathers of much the same character as those along the tail, and nearly, though not quite, of the same length . . . . Prof. Marsh has, indeed, already suggested that the power of flight probably originated among the small arboreal forms of reptilian birds, and has instanced the flight of *Galeopithecus,* the flying squirrels (*Pteromys*), the flying lizard (*Draco*) and the flying tree-frog (*Rhacophorus*) as indicative of how this may have commenced. Should it eventually prove to be the case that there were what may be termed supplementary wing-feathers on the hinder extremities of such early forms of birds as the Archaeopteryx, his views as to the origin of the powers of flight will be satisfactorily confirmed."

Under the heading "Das Federkleid," Dames devotes considerable space to these tibial feathers. He admits them as

[1]Quite unconnected with the present thesis, but interesting as a sentiment expressed thirty-six years ago, the following paragraph by Vogt is worthy of note: "M. Volger se berçait dans l'espérance que S. M. l'empereur Guillaume achèterait la piecè (Archaeopteryx) pour la conserver à l'Allemagne. Sa Majesté n'entra pas dans ces vues. Ah! si au lieu d'un oiseau, il s'etait agi d'un canon ou d'un fusil pétrifié!"

*culottes* or what we would call a booted feathering, but denies their function as assisting in flight. Without following his involved arguments, he says in part:

"Zunächst ist es nicht richtig, dass diese Federn dieselbe Consistenz gehabt haben, wie die des Flügels und des Schwanzes, denn sie sind weit undeutlicher erhalten, auch beträchtlich kürzer (Länge durchschnittlich 32 mm. lang) als die Schwanzfedern, welche im mittleren Theil des Schwanzes ungefähr 65 mm. lang sind; . . . . sondern halb so lang . . . . Wenn man aber trotz alle dem doch noch an der Möglich keit, dass Archaeopteryx auch mit den Hinterbeinen geflogen sei, festhalten wollte, so wäre dem noch entgegenzuhalten, dass diese Eigenschaft nothwendig auch irgend welchen Ausdruck im Bau der Knochen der Hinterextremitäten erlangt haben müsste."

The two most recent commenters on this subject differ as completely as do Evans and Dames. Abel in his interesting subheading of "Die mangelhafte Ausbildung des Flugvermögens von Archaeopteryx," writes: "Die zweizeilige Befiederung der Unterschenkel spricht dafür, dass diese Federn den Flug der Archaeopteryx als Fallschirmapparate unterstützt haben."

Heilmann, writing in Danish, gives his opinion in an equally pithy phrase; "it is improbable that the feather coating on the tibia (as assumed by some authors) was of any importance in flight, as it appears too weak.[1]"

## Part III.—Argument.

The pelvic alar tract as I have found it in modern birds is remarkably uniform in position, originating on the anterior outer side of the tibia below the knee, and extending back, along the femoral patagium, to the body and toward the tail. The feathered patagium between the extended leg and the body must have been of the greatest importance, for the feathers sprouting in this area in the young bird are of very large size and invari-

[1]Altsaa rimeligvis paa Overgangen mellem Faldskaermssvaeven (som vi f. Eks. traeffer den hos Flyveegern) og ubehjaelpsom Flagreflugt.

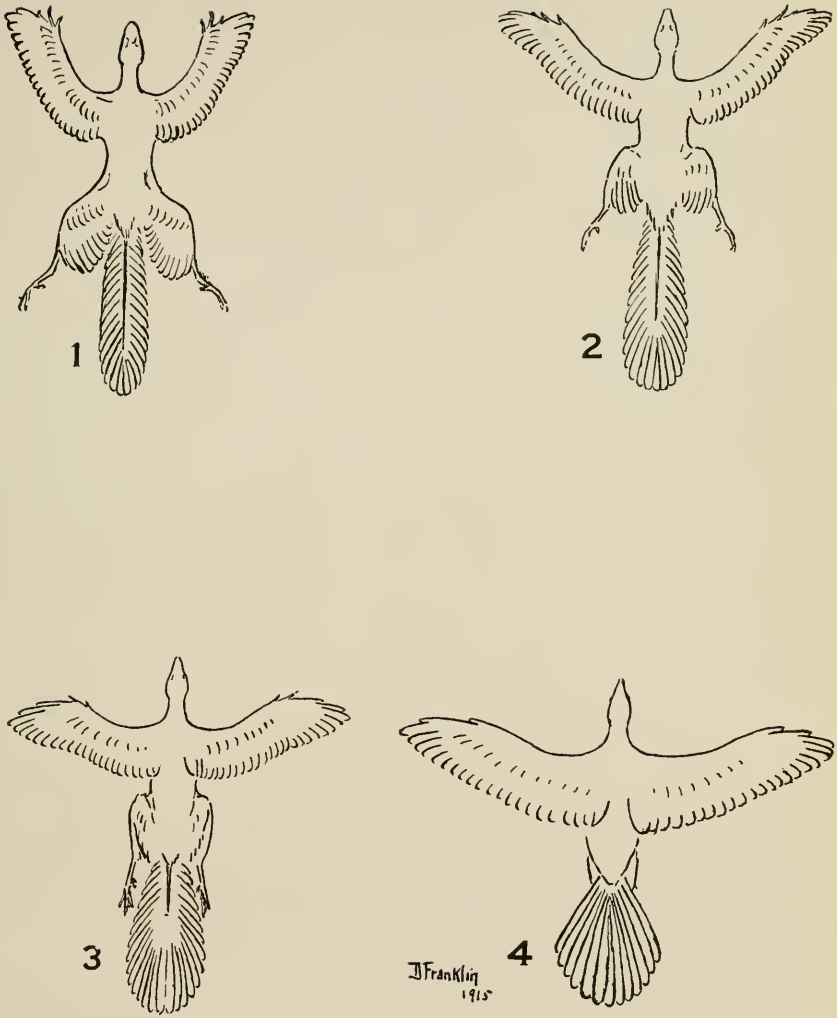


FIG 11. THE EVOLUTION OF BIRDS FROM THE TETRAPTERYX STAGE (No. 1), THROUGH ARCHAEOPTERYX-LIKE STAGE (No. 2), TO THE MODERN BIRD (No. 4).

The principal changes were the feathering and mittening of the fingers; the great strengthening and centralizing of the pectoral wing; the correlated reduction of the femoral or pelvic wing; the shortening of the tail and the concentration of the tail-feathers

ably provided with coverts. This is the pterylum which we hope to find paralleled or directly represented in Archaeopteryx.

The most cursory examination of the fossil reveals the beautifully preserved wing and tail-feathers. Very faint and not at all certain traces have been thought by several observers to represent a ruff of soft feathers at the base of the neck. We have already seen the diverse opinions which the two rows of tibial feathers have aroused. Besides these feathers there have been noted traces of small, soft, covert-like feathers covering the bases of the wing and tail feathers. The remainder of the body has, wholly without reason, been adjudged as scaly. On circumstantial evidence, but equally improbably, others have considered it as quite naked. The most reasonable hypothesis is that the body was fully clothed in soft, rather downy plumage. When the bird died, it fell upon the mud of some river or shore and there, like the remains of gulls which we may find today, it was slowly disintegrated by the elements to a point where all the soft, body plumage was detached and washed or blown away. At the time of being imbedded in the fine silt it retained only the strongly socketed wing and tail feathers and those clinging to the hinder extremities.

The most perfectly preserved part of the London specimen of Archaeopteryx is the tail. From base to tip it is almost without a flaw, and the relative length and position of the feathers are as distinctly seen as in the living bird. The outline of the tail as a whole is like that of a broad, truncated feather, tapering gradually to the base. I mention these details in order to compare them with those of the tail in the Berlin specimen of Archaeopteryx. Here the tip of the tail is lost, but the base is quite distinct. We can observe the same gradual narrowing, due to the increasing shortness of the feathers toward the pelvis. Between the bent-back head and the pelvis, however, we see impressions of feathers which are longer than any at the base of the tail. Their origin is indefinite, somewhere near the pelvis or femur, and they arch up and backward as distinctly as many of the tail-feathers themselves. It seems reasonable to me that this group of feathers, which somewhat resembles a diminutive

wing, may represent the pelvic alar tract which is so remarkably developed in modern squabs.

This character is plainly visible in any good photograph of the Berlin Archaeopteryx. Lankester[1] shows it very distinctly in his reproduction of the fossil. As to the much-discussed tibial feathers, I agree with Evans and Abel that they seem too pronounced in outline to be classed with the downy feathers such as we see on our booted falcons. I think they are the distal elements of the pelvic wing, of far less importance as a *fallschirmapparate* than the larger feathers near the pelvis, which probably arose from the femoral patagium. Most students of this bird have ignored these tibial feathers and in restorations they are usually omitted. Miss Woodward in her artistic plate[2] shows them as soft and fluffy.

Heilmann has approached the general subject of the origin of birds in a most delightful manner. His illustrations show real imagination, using that much abused word in its most admirable sense. Unfortunately his Danish text limits the possibility of wide appreciation. While, as I have shown, he does not believe that the tibial feathers were of volant function, yet, curiously enough, in his very original and dramatic restoration of Archaeopteryx,[3] he has indicated a line of large feathers near the pelvis, which in position correspond to the inner feathers of my pelvic wing.

The argument of Dames against the possibility of the hind leg functioning in aerial activity is at fault. It is naturally impossible to conceive of a skilful flier, flapping with both arms and legs, and with ability for sustained and directive flight, to have evolved such a complicated dermal apparatus without corresponding changes in muscles and bones. But in Archaeopteryx or in our prejurassic Tetrapteryx, the function of the pelvic wings would have been merely passive parachutes. In this early stage, as probably also in Archaeopteryx, flight was merely gliding or scaling. The fingers were too free, the arm bones too delicate, the sternum small or absent, and these facts considered in

[1]Extinct Animals, 1905, p. 238.

[2]Evolution in the Past, Knipe, 1912, p. 96. (II).

[3]Vor Nuvaerende Viden om Fuglenes Abstamning, fig. 11.

connection with the small, weak pelvis, makes it impossible to picture the bird as flying skilfully about.

In earlier, lizard-like, aboreal forms, the scale-anlagen of the wing feathers were correlated with corresponding developments along the hind leg, the two increasing equally in size and evolving feather lightness with change in structure.

Even in Archaeopteryx, with its broad, excellent wing, the hand shows little or no correlated adaptation. The absence of two digits has probably no avian, or certainly no volant significance, for we find identical conditions in the manus of carnivorous, bipedal but terrestrial dinosaurs, such as Ceratosaurus, Ornithormimus and Ornitholestes.

If we admit Archaeopteryx to the direct line of lizard—Tetrapteryx—bird geneology, we must conceive of it as having reached a stage where the pectoral wing was becoming dominant, and beginning to afford support to the creature in general. The elongated flight feathers were now extending backward and superceding the passive function of the pelvic wing. With this concentration of motive and supporting power was soon to be correlated a shortening and reduction of the long unwieldy tail.

In succeeding generations the pelvic wings would become more and more reduced. Having arisen from among the surrounding scales, they had, for a time, volplaned through the air of early ages, a character passive and, as future centuries would show, of merely transitory function. Yet they were of tremendous importance in allowing the pectoral scales to develop, to become feathers, and then to assume an importance which was to make the class of birds supreme in the air. Yet the function of the pelvic wings had been so passive and negative that no special muscling had been necessary, no increase nor coalescence of bony tissue. Little by little the line of feathers and their coverts sank again into insignificance and became lost among the body plumage. It affords an excellent example of what Professor Henry F. Osborn would call the phylogenetic accelleration of a character, followed by its gradual reduction.

Millions of years after they were of use, the feathers of the pelvic wing are still reproduced in embryo and nestling. And

for some unknown reason, Nature makes each squab pass through this Tetrapteryx stage. The line of feathers along the leg of the young bird reproduces on this diminutive, useless scale the glory that once was theirs. No fossil bird of the ages prior to Archaeopteryx may come to light, but the memory of Tetrapteryx lingers in every dove-cote.